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ARTICLE

Postrelease exploration and diel activity of hatchery, wild, and hybrid strain brown trout in seminatural streams

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Abstract: Behaviour that is adaptive in captivity may be maladaptive in the wild and compromise postrelease survival of hatchery fish. The understanding of behavioural variation displayed immediately after release could help to improve hatchery protocols and development of behavioural tests for assessing the fitness of fish reared for releases. We characterized the postrelease behaviour of common-garden-raised offspring of wild resident, captive-bred migratory, and hybrid brown trout (*Salmo trutta*) in two experiments: in small artificial channels and in high and low densities in seminatural streams. The results from seminatural streams showed that hatchery fish were more likely to disperse downstream from the initial stocking site compared with hybrid and wild strain fish. The small-scale experiment did not reveal this ecologically pivotal difference in postrelease performance among strains, and individual responses were inconsistent between the experiments. Circadian activity patterns did not differ among strains. These detailed observations of postrelease behaviour reveal important intrinsic differences in dispersal traits among brown trout strains and suggest that selective breeding and crossbreeding can substantially affect these traits.

Résumé : Un comportement bien adapté à la captivité pourrait s'avérer mal adapté dans la nature et compromettre la survie de poissons d'écloserie après leur lâcher. La compréhension des variations comportementales présentées immédiatement après le lâcher pourrait aider à améliorer les protocoles d'écloseries et la mise au point de nouvelles épreuves pour évaluer l'aptitude des poissons élevés pour être relâchés. Nous avons caractérisé le comportement après le lâcher de progéniture élevée en jardin commun de truites de mer (*Salmo trutta*) résidentes sauvages, migratrices élevées en captivité et hybrides dans deux expériences, à savoir : dans de petits chenaux artificiels et dans des cours d'eau semi-naturels, à forte et faible densités. Les résultats pour les cours d'eau semi-naturels montrent que les poissons d'écloserie étaient plus susceptibles de se disperser en aval à partir du site d'empoissonnement initial que les poissons hybrides et de lignée sauvage. L'expérience à petite échelle n'a pas fait ressortir cette différence clé sur le plan écologique de la performance après le lâcher entre les lignées, et les réactions individuelles n'étaient pas cohérentes d'une expérience à l'autre. Les motifs d'activité circadienne des différentes lignées ne présentaient pas de différence. Ces observations détaillées du comportement après le lâcher révèlent des différences intrinsèques importants des caractères associés à la dispersion entre différentes lignées de truites brunes et indiqueraient que la reproduction sélective et le croisement peuvent avoir une incidence considérablement sur ces caractères. [Traduit par la Rédaction]

Introduction

Enormous numbers of captive-bred, hatchery-raised fish are released worldwide to support fisheries, enhance weakened natural populations, or introduce new fish populations (Cowx 1994). Yet the stockings too often fail to improve the actual fisheries or the conservation of the endangered populations (Naish et al. 2007). Long-term captive breeding can result in fitness loss of the reared fish in natural conditions (reviewed by Fraser 2008), often resulting in acute or long-term failures in compensation and restoration programs (Lorenzen et al. 2012; Glover et al. 2018). To increase stocking success, it is necessary to understand the mechanisms explaining the low postrelease survival rates. Simplified hatchery environments may favour phenotypes that display, for instance, impaired antipredatory behaviours (Petersson and Järvi 2006), increased boldness (Sundström et al. 2004), or fast growth that increases risk-taking behaviour (Biro et al. 2004; Biro and Post 2008; Saikkonen et al. 2011). When the aim is to reintroduce a naturally reproducing population, controlled crossbreeding of hatchery brood stocks, often used for stockings in large geographical areas, with locally caught wild fish might provide a solution to increase fitness of the stocked fish in local environments (Houde et al. 2015).

Owing to the drastic difference between hatchery and wild environments (Huntingford 2004; Johnsson et al. 2014), the short time period following release to nature represents a major habituation challenge with critical survival implications. Multiple experiments have compared the postrelease survival among fish from hatchery, wild, and hybrid origins (Berg and Jørgensen 1991; Jonssonn et al. 1999; Jokikokko et al. 2006; Dahl et al. 2006; Pinter et al. 2017), but sole recapture data are insufficient to answer what behavioural mechanisms might explain the observed differences. Acute survival of stocked fish depends often on postrelease behav-

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iour (Huntingford 2004; Johnsson et al. 2014), but studies focusing on detailed behavioural mechanism provoking survival differences are scarce (Rodewald et al. 2011; Rodewald 2013). Stocking experiments performed in natural systems have shown that hatchery-reared parr (riverine juvenile) move farther downstream than wild parr immediately after release (Jørgensen and Berg 1991). Brunsdon et al. (2017) showed that stocking density alters spatial distributions so that a high stocking density increases downstream dispersal distance from the stocking site. Likewise, low-density releases have been shown to result in higher survival rates compared with high-density releases (McMenemy 1995). The cost of territoriality in high density may exceed the benefits (Bohlin et al. 2002). Thus, as an adaptation to high-density conditions, hatchery-bred fish may display impaired territorial (Fenderson and Carpenter 1971) and unnatural schooling behaviour (Ruzzante 1994) that potentially results in downstream dispersal and survival cost in the wild.

Another behavioural trait potentially affected by multigenerational captive breeding is the activity rhythm of the fish. Captively-bred brown trout (*Salmo trutta*) are found to be more day-active than wild trout (Álvarez and Nicieza 2003). Behavioural activity of wild salmonids follows a circadian rhythm — feeding rates are low during the night when visibility is low and at midday when predation risk and light intensity are high (Hoar 1942). Circadian rhythmicity is an adaptation to environmental selection pressures such as predation risk, food availability, and thermal regimes (Yerushalmi and Green 2009), driving salmonids to crepuscular foraging activity (Hoar 1942). In hatcheries, such rhythmicity is often lost as food is usually available at daytime or fish may use all hours for foraging. Thus, hatchery-reared fish may face increased predation risk in nature due to maladaptive activity patterns (Metcalfe et al. 1999; Álvarez and Nicieza 2003). Therefore, it is important to consider full diel cycles when studying consistent behavioural differences among individuals (Závorka et al. 2016), and potential differences between hatchery and wild fish.

Here, we experimentally studied individual differences in post-release behaviour in relation to the genetic strain of the fish using common-garden-reared 1-year old brown trout parr. We used pure and reciprocally crossbred fish from two originally philopatric populations: (*i*) migratory hatchery strain that has been bred in captivity for decades and is virtually extinct in the wild due to intensive fishing and (*ii*) moderately genetically differentiated wild resident population from a small upstream stream (cf. Lemopoulos et al. 2019*a*). We hypothesized that the hatchery population would represent a more (downstream) dispersive phenotype and display higher daytime activity than the wild strain, while the hybridized fish were expected to show an intermediate phenotype. We quantified individual plasticity in postrelease behaviour in two experimental contexts using behavioural reaction norms (Dingemanse et al. 2010) and aimed to test whether a small-scale experiment in small groups could predict individual behaviour in ecologically more relevant context and in larger groups. Further, we expected that density manipulation would result in increased dispersal in a high-density treatment, in particular in the hatchery strain fish due to poorer capacity to defend territories compared with the wild strain fish. The hatchery strain fish were expected to show high activity and rather unimodal circadian activity patterns, while wild strain fish were expected to obtain bimodal circadian activity patterns sooner after release. Hybrid fish were expected to display intermediate responses.

Materials and methods

Fish

Experimentally bred fish originating from a headwater river Vaarainjoki (wild strain, mainly resident) and larger rivers Varisjoki and Kongasjoki in the same watercourse (hatchery strain, mainly adfluvial; for smolt migration differences see Lemopoulos et al. 2019*b*) were reared in common garden conditions prior to the experiments at Kainuu Fisheries Research Station (KFRS, www.kfrs.fi) of Natural Resources Institute Finland (LUKE) (see also Alioravainen et al. 2020). Despite the very short (<1 km) distance between the rivers, these two populations show some genetic divergence (pairwise genetic difference F_{ST} = 0.11; Lemopoulos et al. 2019*a*). River Vaarainjoki as well as River Kongasjoki discharge to Lake Kivesjärvi (27 km^2, ~0.5 km apart from each other), which is connected to a major (928 km^2) lake (Oulujärvi) via River Varisjoki (64°16′34″N, 27°12′18″E). The founders of the hatchery brood stock, established in 1960s and replenished with wild fish until 1980s, were adfluvial brown trout captured in River Varisjoki and River Kongasjoki. The contemporary brood stock has been maintained in captivity for conservation and stocking purposes by LUKE since the pooling of three original hatchery strains maintained by different hatcheries in year 2000. The parent fish used in this study represented fourth–fifth generation of captive-bred adults. The wild parent fish were captured by electrofishing during spawning time in 2010–2012 from River Vaarainjoki and maintained in two 50 m^2 gravel-bottomed rearing ponds (in size-assorted groups). Hatchery strain parents were reared in two 75 m^2 concrete rearing ponds prior to breeding (Alioravainen et al. 2020).

For this study, we used F_1 generation pure strains produced using three female × three male full factorial breeding design (36 adults in hatchery and 36 adults in wild strain in total, three half-sib matrices per angling selection line that were equally pooled; see Alioravainen et al. 2020) and both hatchery female × wild male and hatchery male × wild female crosses (six adults per strain per sex, 24 in total, two half-sib matrices per direction). From each half-sib family, 100 eggs were incubated over winter, and thereafter 25 fry from each family were aimed to be pooled within each breeding matrix (but mortalities were compensated by taking more than 25 fry from some families as equally as possible) and reared in the density of 225 fish·tank^{-1} in two replicates in 0.4 m^2 tanks. In September 2016, ~6 months after hatching, the fish were tagged with 12 mm half-duplex PIT tags (Oregon RFID) (in the body cavity through a small scalpel-made incision) under anaesthesia (benzocaine 40 mL·L^{-1}). We maintained the tagged fish in two 3.2 m^2 glass fibre hatchery tanks (n = 450·tank^{-1}) and fed them ad libitum with commercial fish feeds using automated feeders until the beginning of the experiments in April 2017. All animal experimentation was conducted under a licence from the national Animal Experiment Board of Finland (licence No. ESAVI/3443/04.10.07/2015).

Experiment in artificial channels

Small-scale behavioural trials in small groups were performed in artificial flow channels (length 6 m, width 0.4 m, depth 0.2 m, flow rate 1.60 L·s^{-1}, with gravel bottom) to quantify individual movements in group context. The trials were conducted between 26 April and 29 May 2017 indoors at KFRS. In each trial, we released 12 fish (n = 4 per strain) to acclimate in a subsection separated with metal grid (mesh diameter (Ø) = 5 mm) in the downstream end of each channel (n = 4) for 48 h before releasing them to explore the whole channel freely for 5 days (120 h; for details see online Supplementary Fig. S1[1]). Altogether, we ran five consecutive trial periods and tested 240 individuals. After each trial, we measured the tested fish for total length (1 mm) and wet mass (0.1 g) under

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0436.

anaesthesia (benzocaine 40 mg·L^{-1}). The groups did not differ in size (ANOVA, $F_{[2, 236]} = 0.35$, $p = 0.7$; hatchery: 121.4 ± 11.2 mm (mean ± SD), wild: 121.4 ± 11.0 mm, crosses: 122.6 ± 10.8 mm). After the experiment, fish were maintained as before the trials until the experiments in the seminatural streams. Fish were measured only once because the interval between experiments was relatively short.

Experiment in seminatural streams

One month after the end of the artificial channel experiment, on 28 June, we introduced the same fish (n_{total} = 240) in eight circular seminatural streams (area = 30 m^2; Fig. S2[1]), located outdoors at the KFRS. The fish were randomly divided into two different densities (n_{low} = 12 fish, 0.4 individuals·m^{-2}, 4 fish per strain and n_{high} = 48 fish, 1.6 individuals·m^{-2}, 16 fish per strain). Fish were fasted for 1 day before they were introduced to flow-through fish chests (0.50 m × 0.80 m, open in the both ends and covered with a grid Ø = 5 mm mesh size) between 22:00 and 01:30 for stress recovery. After 14.5–18 h acclimation time in the chests, they were released into the stream at 16:00.

Every pool had a gravity-driven flow (40.5 L·s^{-1}, ~0.9 m·s^{-1}), water depth of 0.30 m, and a similar setup to monitor fish movement: four PIT antennae loops across the whole riffle in every quarter of the pool (Fig. S2[1]). The water temperature and oxygen content varied naturally within ranges 12.7–14.8 °C and 8.0–8.5 mg·L^{-1}, respectively. The circular riffle section was 26.15 m long (from the middle) and 1.5 m wide. During the experiment, the natural day length in the area was 21 h 15 min from 02:35 to 23:50. We did not feed the fish with any additional food, since the pools had rich benthic macroinvertebrate fauna and drift along the incoming water (Rodewald et al. 2011). All pools were covered with a tent canvas to prevent avian predation and provide shelter from direct sunlight. As in the artificial channel experiment, we monitored individual movements for the 5 first days in the channels, after which the fish were left in the seminatural streams for further data collection (not used in this study).

Statistical analyses

The automatically collected raw PIT data were configured using TIRIS data-logger program (Citius Solutions Oy, Kajaani, Finland; see details in Vainikka et al. 2012). Antenna-specific ASCII data were further aggregated to form movement data on 1-second resolution using software PIT-data (www.pitdata.net). From the processed 1-second-interval PIT-data, we analysed individual movements based on antennae bypasses per hour. Only antennae readings from a different location than the previous reading were considered as a movement. Further movement data processing was performed using self-made scripts (by N.A.) and tidyverse package collection (version 1.2.1; Wickham 2017). All the analyses were performed using R (version 3.5.2; R Core Team 2018) through R Studio (RStudio Team 2016). Annotated scripts and data are available online (Open Science Framework; osf.org; doi:10.17605/OSF.IO/BNA59).

We fitted linear mixed effects models with random slope (i.e., random regressions, LME, lme4 package, version 1.1-21; Bates et al. 2015) to model individual movements separately in each experiment. To analyse within and between variance of individual, random intercept was modelled for each fish and experiment day was used as a random slope to capture the plasticity effect. In the model for the seminatural stream experiment, pond ID was confounded with the density treatment and nesting was not possible due to low number of replicates, but it was used as a random factor (as representing also temporal replicates) in the model for the artificial channel experiment. We tested the fixed effects of strain and density (high versus low) in seminatural streams on total daily activity of the individuals (individual antenna bypasses per day). Individual length was used as a linear covariate, as length could explain swimming capacity. Experiment day was a fixed term to capture the overall trend, as it did not violate the assumption of the homoscedasticity of the LME residuals, and was a random variable to capture individual variance within time. We standardized movement measures from artificial channels and seminatural streams to make them comparable (to have mean of 0 and SD of 1). Finally, we estimated the 95% confidence intervals of model parameters based on 10 000 posterior simulations by using arm package version 1.10-1 (Gelman and Su 2018). Type II ANOVA was used to test the statistical significance of the differences among group means within fixed effects by using functions in lmerTest package (Kuznetsova et al. 2017).

To quantify the context dependency of individual behaviour (i.e., responses in the tested environments), repeated within-individual measures within each context were needed (Araya-Ajoy et al. 2015). First we quantified the narrow sense repeatability, R^2_{GLMM}, of individual behaviour based on random slope LME models using an approach introduced in Johnson (2014). After testing the repeatability of individual behaviour within each context, we used one best linear unbiased predictors (BLUP) per individual per experiment to compare within-individual responses. Individual reaction norms can be estimated from random slope regression models, where individual predictions (BLUP) for behaviour are determined as random intercepts from GLMM fitted separately for the two experiments (Dingemanse et al. 2020). Finally, the regression line between the two context-dependent BLUP formed the individual reaction norms (Dingemanse et al. 2010).

All visualizations were made using ggplot2 package (version 3.2.1; Wickham 2017). To visualize and model how movement patterns changed over experiment days among strains, we used nonparametric Loess regression that uses local weighted regression to fit a smooth curve through points in a scatter plot. If estimated 95% confidence intervals of Loess fitted curves did not overlap, the differences were considered statistically significant.

For clarification, we considered downstream movement as "dispersal", because fish relocate themselves from their stocking site. To-and-fro type of movement in artificial channels was considered as "exploration", because the movement did not relocate the fish per se.

Results

Effects of size and time on moving tendency

Experiment day had a clear negative effect on daily total movements, showing that highest movement rate occurred immediately after the release (Table 1; Fig. 1). The slopes of ID were close to zero (Table 1), which indicates that the movement patterns in general were similar within individuals. Individual body length had a significant positive effect on movement in the artificial channels but no effect in the seminatural streams (Table 1).

Effects of strain and density on moving tendency

In the seminatural streams, the direction of the movement was mainly directed downstream in all strains (Fig. S3[1]). In the seminatural streams, strain had a clear effect on behaviour; hatchery strain fish showed the highest dispersal tendency and wild strain fish the lowest (Table 1). Low density intensified the dispersal tendency in seminatural streams (Table 1). Loess regression curves confirmed that in the artificial channels there were no clear differences among the groups in exploration, but in the seminatural streams, divergent dispersal patterns clearly emerged between hatchery and wild strains (Fig. 1). In high density, hybrid and hatchery strain fish were similar and dispersed more than wild strain fish, whereas in low density, hatchery strain fish showed much higher dispersal tendency than wild strain fish until the end of the experiment (Fig. 1).

Table 1. Summary of linear mixed effects model of total individual movement activity based on five measurements (days) of 239 individuals in two experiments.

Responsive variable	Effect					
Moving tendency in artificial channels	Random		Mean σ^2	SD		
	Fish ID	Intercept	0.417	0.646		
		Day	0.005	0.069		
	Channel	Intercept	0.254	0.504		
		Day	0.009	0.094		
	Residual		0.491	0.401		
	Fixed	df_{num}, df_{dem}	F	p	Estimate	95% CI
	Intercept				0.037	−0.281, 0.352
	Experiment day	1, 18.999	67.254	<0.001	−0.211	−0.262, −0.160
	Fish length	1, 222.028	42.837	<0.001	0.021	0.015, 0.028
	Strain	2, 216.028	1.438	0.240		
	Hatchery				0.140	−0.025, 0.301
	Wild				0.058	−0.107, 0.223
Moving tendency in seminatural streams	Random		Mean σ^2	SD		
	Fish ID	Intercept	1.711	1.308		
		Day	0.071	0.267		
	Residual		0.187	0.432		
	Fixed	df_{num}, df_{dem}	F	p	Estimate	95% CI
	Intercept				0.770	0.517, 1.030
	Experiment day	1, 238	223.011	<0.001	−0.289	−0.327, −0.251
	Fish length	1, 234	1.550	0.214	−0.004	−0.010, 0.002
	Strain	2, 234	12.544	<0.001		
	Hatchery				0.341	0.178, 0.503
	Wild				−0.043	−0.208, 0.120
	Density	1, 234	30.058	<0.001		
	Low				0.476	0.3081, 0.649

Note: Fixed effect estimates and confidence intervals were estimated based on 10 000 posterior simulations of β from LME model. Hybrid group and high density set the intercept. Type II ANOVA-based F statistics and their p values indicate the among-level differences in means within fixed effects and statistical significance.

Fig. 1. Loess regression curves showing strain-specific movement activity (antenna bypasses) in the artificial channels (left) and total moving activity (rounds moved in circular riffle) in seminatural streams in high and low densities (right). Experiment day was used as a covariate. Different lines show mean activity of strain. Grey areas indicates 95% CI.

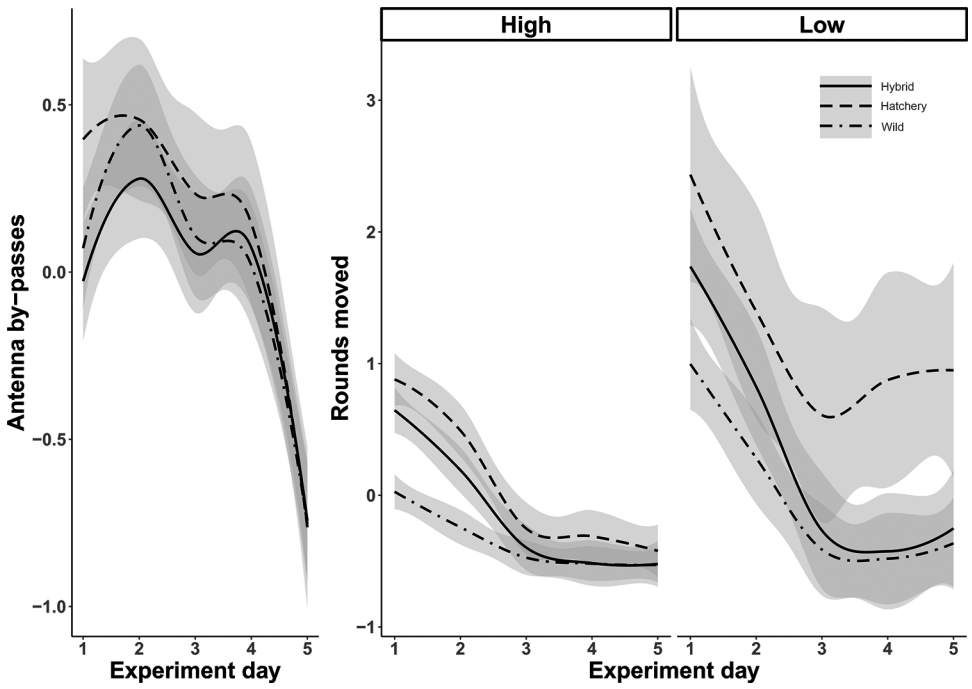
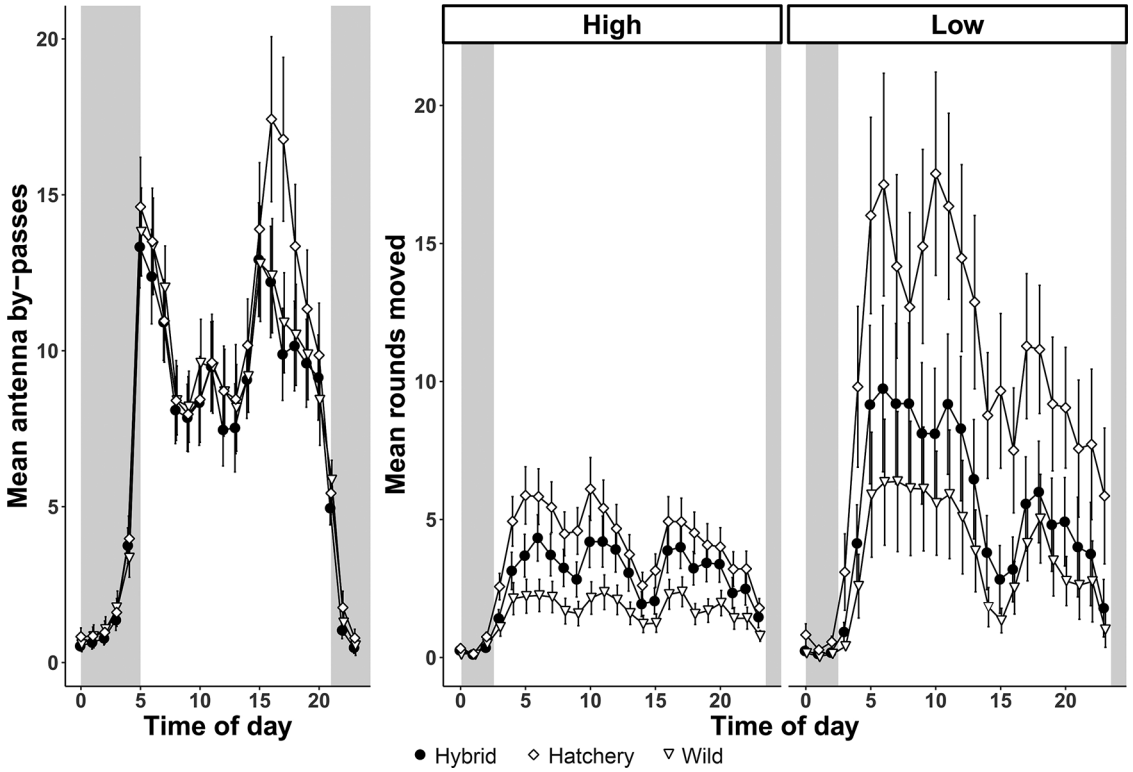


Fig. 2. Mean antenna bypasses per clock hour over five consecutive diel cycles in the artificial channels (left) and seminatural streams in high and low densities (right). Whiskers indicate 95% CI. Dark period (left) and time between sunset and sunrise (right) are indicated with grey shading.



Individual plasticity in moving tendency

The individual behavioural responses (as BLUP) were found to be repeatable within the context: $R^2_{GLMM} = 0.48$ and 0.80 in artificial channels and seminatural streams, respectively. Nevertheless, individual behavioural responses were not found to correlate between experiments (Pearson's $r = 0.03$, $t = 0.51$, df = 237, $p = 0.61$; Fig. S4[1]). Individual behavioural reaction norms indicated that extreme phenotypes may express the opposite behaviours in different contexts (Fig. S5[1]).

Circadian patterns

Very similar circadian activity patterns were found in both experiments. The fish showed bimodal activity patterns, where highest peaks occurred after 05:00 in the morning and again in the afternoon between 15:00 and 20:00 (Fig. 2). In the seminatural streams, fish began to be active at sunrise (Fig. 2). In the artificial channels, the only difference in activity among the groups occurred during the afternoon, when hatchery strain fish were slightly more active than hybrid and wild strain fish (Fig. 2). In the seminatural streams, hatchery strain fish were more active than wild strain fish during every hour when the fish were moving (Fig. 2). Hybrid fish displayed average phenotypes compared with wild and hatchery strain fish (Fig. 2). In the low-density treatment, the patterns were similar to those at high density, but peaks were much higher, indicating high overall rates of antenna bypasses per hour (Fig. 2). Individual circadian curves showed that there were no distinctly night-active individuals (Fig. S6[1]).

Discussion

Our study provides a potential behavioural and ecologically relevant explanation for acute failures in the stocking of captive-reared fish. We showed that the phase of high moving activity lasts at least two full diel cycles after release, but the intensity of the initial high dispersal period can be strain-dependent. Hatchery strain parr swam farther downstream than other strains, indicating that they will likely not stay near their stocking site but disperse rapidly. Against our expectations, low density further intensified downstream movement of hatchery strain fish in the seminatural streams. That parr movement occurs mainly downstream from original stocking site aligns with the predictions from Jørgensen and Berg (1991) and Brunsdon et al. (2017). The experiment in the artificial channels did not reveal any differences among strains but confirmed the presence of high acute postrelease activity as a reaction to unfamiliar environment (Závorka et al. 2015). Nevertheless, at the population level, the average individual responses to the two environments were uncorrelated and indicative of strong gene × environment interactions (Dingemanse et al. 2010). All fish displayed bimodal circadian activity patterns quickly, but the hatchery strain fish showed the highest activity in both experiments and independently of the time of day, as expected.

Large-sized fish displayed increased movement in the artificial channels, but individual size had no effect on moving tendency in the seminatural streams, suggesting that there is no clear correlation between individual size and dispersal tendency or that swimming capacity was not a limiting factor in setting dispersal behaviour. Thus, stocked hatchery fish can have high dispersal tendency in seminatural streams as an avoidance towards a novel environment or if they cannot successfully compete for limited resources, which may further predict high mortality in the wild. Hatchery strain parr moved strongly downstream on the first day after release. Interestingly, low density further increased the dispersal tendency of hatchery strain fish compared with high density. The circular streams can increase the distance swum, as fish do not reach a new habitat and hence may not know when to settle down. Even so, some of the fish were very determined in their downstream movement that it could potentially be considered as downstream (presmolt) migration (~12 km·day^{-1}). It could

be that the stress from stocking and novel environment with running water can trigger downstream dispersal.

Release to the wild, or translocation of animals in general, can be considered a major human-induced environmental change and dispersal an avoidance reaction to the novel environment (Sih et al. 2011). Interestingly the wild strain fish did not disperse as far downstream, indicating to-and-fro type of explorative behaviour in a novel environment (Réale et al. 2010). While exploratory behaviour can be risky under natural conditions by increasing vulnerability to predation (Hulthén et al. 2017) and fishing (Biro and Post 2008; Härkönen et al. 2014), it can facilitate habituation (Adriaenssens and Johnsson 2013; McCormick et al. 2018). Introduced wild fish are better at habituating in their stocking site and establishing their territory, whereas hatchery fish may show unnecessary aggressions towards conspecifics and have problems with finding territories (Deverill et al. 1999). As a result, hatchery juveniles displace themselves from their stocking site, which makes them vulnerable to predation, decreases the likelihood of finding a suitable habitat, and increases mortality in the wild (Elliott 1989). Because the density treatment did not affect the main movement direction, it seems that fish prefer to disperse downstream in general. Owing to limited resources in enclosures, individuals may be forced to continue searching downstream (Grant and Kramer 1990; Grant et al. 2017). The indication of reactivation of dispersal in hatchery strain fish in low density suggests that individuals that are unable to occupy territory in a new habitat must continue dispersal farther to seek a free territory. The high density potentially facilitates the settling of individuals and decreases dispersal, probably by reducing territorial behaviour of dominant individuals and (or) reducing the postrelease stress as they are deferred to high densities in the hatchery. If this is the case, stocked fish may later begin to redistribute if competition in the stocking site intensifies.

Hatchery, hybrid, and wild strain fish displayed a natural activity rhythm and showed bimodal circadian activity already within the first diel cycle after release in both experiments. Hence, it is unlikely that adopting natural circadian rhythms could be problematic for stocked fish. Hatchery strain fish were moving more than wild strain or hybrid fish at any time of day they were active. The observed high diurnal activity rates of hatchery strain fish may associate with high energy demands, as stocked fish rapidly start foraging also in their new environments (Rodewald et al. 2011). High diurnal activity rates may potentially increase the risk to predation (Werner and Anholt 1993) and vulnerability to fishing (Alós et al. 2012; Härkönen et al. 2014), which may contribute to the low survival rates of hatchery fish in the wild. Changes in diel cycles can occur due to individual growth, for example, when juvenile fish increase diurnal activity as a response to high energy demands (Metcalfe et al. 1998). Indeed, individual growth rates may correlate positively with diurnal activity scores in laboratory trials, leading to high survival rates in the wild (Závorka et al. 2015, 2016). Despite summer nights being bright in northern Finland, where the experiment took place, we did not observe a shift to nighttime activity in juvenile brown trout. A longer period of resource competition might be required for inactive fish to shift circadian rhythm (Závorka et al. 2016).

The lack of correlation between individual BLUP indicates that behavioural experiments in an artificial small-scale environment may fail to explain individual-level responses in near-natural-scale contexts. Individual behavioural reaction norms showed that individual responses were inconsistent between contexts, indicating phenotypic plasticity (Dingemanse et al. 2010). The high within-context repeatability of behaviour but strongly crossing individual reaction norms strongly indicate environment-dependent individual responses, which warns against using behavioural measures obtained in captivity to predict fitness in the wild. Personality-related behavioural responses are expected to be context-dependent (Killen et al. 2016; Horváth et al. 2017; Houslay et al. 2018); thus, artificial environments, especially those that restrict scale-dependent individual movements, may not always reveal ecologically relevant responses (Niemelä and Dingemanse 2014; Závorka et al. 2015; Näslund et al. 2015; Polverino et al. 2016). In general, small scale can restrict movements (Näslund et al. 2015), and a mesocosm that mimics natural environment is likely more stimulating to the fish than a plain, small channel, resulting in phenotypic plasticity between context (Dingemanse et al. 2010).

Although the behavioural development of fish is generally very plastic and can acclimatize to environmental conditions, the lack of complexity in the hatchery environment and the lack of predation-induced natural selection in hatcheries can cause unintended domestication in hatchery brood stocks (Lorenzen et al. 2012). Domestication may decrease fitness in the wild due to maladaptive behaviours (Johnsson et al. 2014), but very little is known on how wild-type brown trout typically disperse and what are the fitness consequences of varying dispersal strategies after release. Our study shows that brown trout strains show genetic differences in their dispersal traits and may thus respond to artificial selection on these traits. The crosses were intermediate in their dispersal traits, showing typical Mendelian response to crossbreeding. Any other effects could be contributed to heterosis effects in the locally adapted Vaarainjoki population or general outbreeding effects in the hatchery strain. For management, this study only shows that dispersal traits are heritable, but any effects attributable to crossbreeding would require introgression for the full evaluation of potential outbreeding depression. Our results add on the empirical evidence of behavioural differences between hatchery and wild strain fish and endorse the importance of source population in breeding programs that aim to support reintroductions and natural reproduction (Houde et al. 2015). To preserve adfluvial brood stock, management can rapidly mitigate some of the behavioural effects of hatchery selection without conflicting migration tendency by mixing locally adapted and naturally selected fish in the brood stock (Kallio-Nyberg et al. 2010). Still, more research is required to determine whether resident wild trout could be used to "rewild" migratory brood stocks so that the growth and migratory characteristics of migratory forms are maintained without substantial negative fitness effects.

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